

# ANALYSING POPULATION NUMBERS OF THE HOUSE SPARROW IN THE NETHERLANDS WITH A MATRIX MODEL AND SUGGESTIONS FOR CONSERVATION MEASURES

Chris Klok<sup>1</sup>, Remko Holtkamp<sup>1,2,3</sup>, Rob van Apeldoorn<sup>4</sup>,  
Marcel E. Visser<sup>5</sup> and Lia Hemerik<sup>2</sup>

<sup>1</sup>ALTERRA, Department of Ecology and Environment, Droevendaalsesteeg 3, P.O. Box 47, 6700 AA Wageningen, The Netherlands

E-mail: chris.klok@wur.nl

<sup>2</sup>Biometris, Department of Mathematical and Statistical Methods, Wageningen University, P.O. Box 100, 6700 AC Wageningen, The Netherlands

<sup>3</sup>Current address: Department of Innovation and Environmental Sciences Copernicus Institute, Utrecht University, P.O. Box 80.115, 3508 TC Utrecht, The Netherlands

<sup>4</sup>ALTERRA, Department of Ecology and Society, Droevendaalsesteeg 3, P.O. Box 47, 6700 AA Wageningen, The Netherlands

<sup>5</sup>Netherlands Institute of Ecology (NIOO-KNAW), Centre for Terrestrial Ecology, P.O. Box 40, 6666 ZG Heteren, The Netherlands

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## ABSTRACT

The House Sparrow (*Passer domesticus*), formerly a common bird species, has shown a rapid decline in Western Europe over recent decades. In The Netherlands, its decline is apparent from 1990 onwards. Many causes for this decline have been suggested that all decrease the vital rates, i.e. survival and reproduction, but their actual impact remains unknown. Although the House Sparrow has been dominant in The Netherlands, data on life history characteristics for this bird species are scarce: data on reproduction are non-existent, and here we first present survival estimates based on live encounters and dead recoveries of marked individuals over the period 1976–2003, 14 years before and 14 years during the decline, reported to the Dutch Ringing Centre. We show that there is an indication that both juvenile and adult survival are lower during the period of decline.

Secondly, to be able to analyse the relative impact of changes in the vital rates, we formulated a general matrix model based on a range of survival values between zero and one with a step size of 0.01 (both juvenile and adult yearly survival) and a range of realistic reproduction values (one, three or five fledglings per pair per year). With the matrix model, we calculated the finite rate of population change ( $\lambda$ ) and applied elasticity analysis. To diagnose the cause of the decline in the Dutch House Sparrow, we parameterised the model with estimates of survival values before and during the decline and present the resulting  $\lambda$ . With the survival estimates from the declining period,  $\lambda < 1$  only if reproduction is relatively low. We discuss this result within the light of available literature data on survival in the House Sparrow. Finally, we evaluate which of the suggested causes of population decline should be reversed to mitigate the decline and how this can be achieved.

**Key Words:** conservation, MARK, matrix model, survival

## 1. INTRODUCTION

The House Sparrow (*Passer domesticus*), a granivorous bird species which is well adapted to agricultural cultivation, has been a common bird in both rural and urban areas of north-western Europe. The species was often perceived as a pest species resulting from its feeding behaviour in crops where flocks of foraging house sparrows can reduce crop yields up to 25% (Summers-Smith, 1963). Nowadays, populations of the House Sparrow are declining rapidly in number in both rural areas and cities in large parts of Western Europe (Vidal, 1997; Summers-Smith, 2000; Hole *et al.*, 2002; Newton, 2004). The decline of farmland birds in general, was especially rapid in the last decades of the 20th century (Siriwardena *et al.*, 1998; Peach *et al.*, 1999; Gregory *et al.*, 2004). This period coincides with a period of intensification of agricultural practices such as land drainage, higher stocking densities, changes in crop varieties, earlier ploughing dates and increased weed-control, which are put forward as the main drivers of bird population decline (Robinson and Sutherland, 2002; Newton, 2004). Population declines have also been described for The Netherlands where populations nearly halved since 1984 (CBS, 2005), and has recently resulted in the addition of the House Sparrow to the Red list of threatened birds ([www.minlnv.nl](http://www.minlnv.nl)).

Hole *et al.* (2002) conclude that the decline of the House Sparrow in rural England most probably resulted from food shortage in winter caused by agricultural intensification. Many factors have been suggested to cause the decline in cities but none has yet been identified as the main cause. Heij (2001) suggests four possible causes for the urban population declines in The Netherlands: (1) a decrease in the number of nesting places resulting from the use of a new type of roof tiles which offers little space for birds to nest, (2) a scarcity in nesting material, because cities have become much cleaner in recent decades, (3) a decline in food abundance for the same reason, and (4) an increase in predation. All of the above suggested causes reduce survival and reproduction of the House Sparrow in some way.

An analysis of life-history data before and during the decline, especially on reproduction and survival, is necessary to clarify the main cause of the decline. Although the House Sparrow has been a common bird, demographic data are relatively scarce and published data on reproduction and survival in The Netherlands are currently lacking for the relevant time periods.

Consequences of changes in reproduction and survival on the finite rate of population change ( $\lambda$ ) can be explored with simple population models such as matrix models. Matrix models are often applied in conservation (e.g. Crouse *et al.*, 1987; Doak *et al.*, 1994; Saether *et al.*, 1999). They are popular given (1) their direct relationship with empirical field data, (2) their clear link between vital rates (reproduction and survival) and population performance ( $\lambda$ ) and (3) the availability of easy-to-use computer packages. Moreover, their relatively low data requirements make them easy to apply (Beissinger and Westphal, 1998).

A special feature of density independent matrix models is elasticity analysis. Elasticity analysis is an analytical tool to assess the contribution to  $\lambda$  of the different matrix elements, which are based on vital rates in the different life stages. Elasticities represent the proportional change in  $\lambda$  given an infinitesimal proportional change in a matrix transition (Caswell *et al.*, 1984; de Kroon *et al.*, 1986). The element with the largest elasticity makes the largest contribution to a change in  $\lambda$ . Elasticity analysis is therefore a useful

tool to assess the potential impact of the suggested causes of decline on the viability of the species.

The purpose of our study was to formulate a general population model to analyse the impact of changes in the values of the life-history parameters survival and reproduction on  $\lambda$ . We applied elasticity analysis to identify which life-history process in which life stage has the largest impact on the finite rate of population change. Our general model is parameterized with survival values (both juvenile and adult yearly survival ranging between zero and one with a step-size of 0.01) and a range of realistic reproduction values (one, three or five fledglings per pair per year). This resulted in an overview of  $\lambda$  and elasticities of yearly juvenile and adult survival probabilities.

The reason why we have chosen an approach with a general model is twofold. First, the scarcity of estimates for survival and reproduction in The Netherlands during and after the decline impedes specific estimates of  $\lambda$  and elasticities. Second, the formulation of a general model can highlight the relative impact of the different life history parameters for species with a similar life cycle.

In this paper, we first present survival estimates for the Dutch House Sparrow estimated separately in each relevant time period. Juvenile (aged <1 year) as well as adult (aged  $\geq 1$  year) survival are estimated on the basis of marked birds recovered dead or encountered alive. Furthermore, to diagnose the cause of the decline in the Dutch House Sparrow, we parameterise the (matrix) model with the estimated survival probabilities before and during the decline, and present the resulting  $\lambda$  and elasticity of the matrix elements. We discuss these results against literature data on survival in this species. Finally, we propose measures that can halt the population decline.

## 2. METHODS

### 2.1. Life History of the House Sparrow

Individuals of the House Sparrow can reach ages up to six (Summers-Smith, 1963) or seven (Heij, 1985) years under natural circumstances, whereas in captivity the age of 12 years has been reported (Kipps, 1953). In a study with ringed individuals in England the average age of the House Sparrow equalled 24 months (Summers-Smith, 1963). Juvenile survival appears to be low, as indicated by Summers-Smith (1963) who reported that 50% of the fledglings died within the first two months of life. The breeding season in northern Europe starts in May and ends in August (Seel, 1968a). The number of broods depends on climatic conditions (Dyer *et al.*, 1977). In a local population in England house sparrows produced one to five broods per year with clutch sizes varying between two and seven eggs (Seel, 1968a, b), which resulted in an average fledgling production of 2.9 per pair per year (Seel, 1970). Juveniles mature in their first year of life and can participate in breeding in their second (Dyer *et al.*, 1977).

The species is strongly sedentary (Lack, 1986; Summers-Smith, 1988; Gibbons *et al.*, 1993). During the breeding season, invertebrates make up a large part of the diet, whereas during the rest of the year crops and weeds are the most important food items (Gramet, 1948; Cramp and Perrins, 1994).

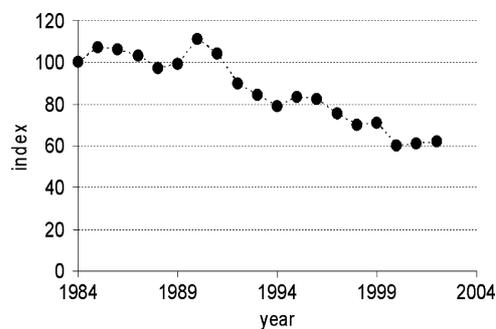
### 2.2. Population Decline and Ringing Data

House sparrows have become relatively scarce in The Netherlands. This resulted in the addition of the species to the Red List of threatened birds ([www.minlnv.nl](http://www.minlnv.nl)).

**Table 1.** Available data on marked house sparrows (recovered dead or re-sighted) of the Dutch Ringing Centre. In the period 1976–1989 1500 individuals were marked and 11007 in the years 1990–2003.

Fate		1976–1989		1990–2003	
		Juvenile <sup>a</sup>	Adult <sup>a</sup>	Juvenile <sup>a</sup>	Adult <sup>a</sup>
Marked as pulli	Recovered dead	12	14	11	7
	Re-sighted	2	1	250	57
Marked as adults	Recovered dead		17		37
	Re-sighted		6		354

<sup>a</sup>Juveniles are individuals marked as pulli and recovered or re-sighted within the year, adults are either marked as pulli and recovered or re-sighted after one year or marked as adult.



**Figure 1.** House Sparrow numbers in The Netherlands (index based on winter-counts, index of 1984 is set to 100; source (CBS, 2005)).

Quantitative data on the decline of the House Sparrow are limited in The Netherlands; the best source is based on data collected by volunteers of the Dutch Centre for Field Ornithology (SOVON) over the period 1984–2003 using the Common Bird Census method (Marchant *et al.*, 1990). The index is set to 100 in 1984 and shows, after some small fluctuations, a steady decline over the period 1990–2002 (Figure 1).

Marked house sparrows have been registered by the Dutch Ringing Centre since 1911 (Van Noordwijk *et al.*, 2003). The Dutch Ringing Centre uses a standardized code to denote all recoveries, dead or alive (Buijs and Thomson, 2001). In the period just before the detected population decline (1976–1990) relatively few birds were registered (see Table 1). Dead recoveries were reported from the whole country, but live encounters only from the provinces Zuid-Holland and Overijssel. Since 1990 house sparrows have been reported and registered on a regular basis and data on both re-sighted and (dead) recovered birds marked as adults or pulli are available from the whole country.

Based on Figure 1 we divided the available data on marked individuals into two time periods of 14 years: the stable period is defined from 1976–1989, and the declining period from 1990–2003. Table 1 shows the available data of marked house sparrows for these two periods.

### 2.3. Statistical Analysis with MARK

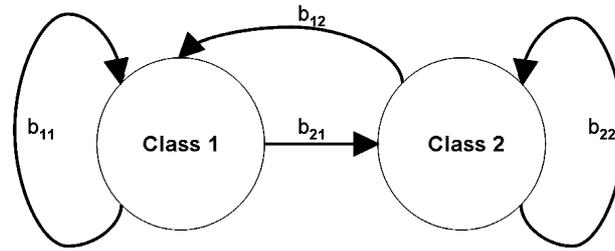
We used Program MARK (White and Burnham, 1999) to estimate the yearly survival of adults and juveniles. Because of the low numbers of recoveries and re-sightings (see Table 1) we used the data type option “Both (Burnham)” in MARK combining dead recovery and recapture data based on the approach first described by Burnham (1993) (see Cooch and White, 2005). Joint analysis of combined data-sets improves the precision of parameter estimates which cannot be achieved by using recoveries or recaptures as single sources separately. We used MARK to fit models consisting of the parameters true survival (S), site (sampling region) fidelity (F), recapture probability (p), and probability of being found dead and reported (r). We modelled these parameters as constants over time (.), grouped by period (p), age-class (c), and period and age-class (p, c). Because the number of dead recoveries and re-sightings per year is low, we did not model parameters varying over time. Our most general model was one in which all parameters are functions of period and age-class (p, c), in MARK code  $(S_{(p,c)}, F_{(p,c)}, p_{(p,c)}, r_{(p,c)})$ . This resulted in four possible states for each parameter, and thus in 256 ( $4^4$ ) possible models. We tested the general model for overdispersion of the data by simulating the model deviance with a bootstrap procedure (bootstrap goodness of fit procedure in MARK). Data are termed overdispersed when there is more variation than predicted by a Poisson or multinomial probability distribution (Agresti, 1990:42). The variance inflation factor ( $\hat{c}$ ) can be calculated by dividing the deviance of the general model by the average deviance from the results of the bootstrap simulations. If  $\hat{c}$  is larger than the critical F-ratio ( $F_{n,k}$ ) at an uncertainty of 0.05 then the data are overdispersed (Crawley, 1993). The degrees of freedom for the F-ratio are the number of observations ( $n$ ) and number of estimated parameters ( $k$ ).

Following the rationale of Burnham and Anderson (2002), we used the modified Akaike’s Information Criterion ( $AIC_c$ ) for model selection, because this criterion gives a weighted value for number of parameters and model fit. It favours parsimonious models and the best model is the one with minimum  $AIC_c$  (Van der Hoeven *et al.*, 2004). When the difference in the Akaike’s Information Criterion ( $AIC_c$ ) of two models is smaller than two ( $\Delta AIC_c < 2$ ) models are considered approximately equal (Cooch and White, 2005). In case of overdispersion of the data  $\hat{c} \gg 1$  the quasi-likelihood modification of  $AIC_c$  the  $QAIC_c$  should be used as a selection criterion (Burnham and Anderson, 2001).

### 2.4. Model Development

We assumed density independent population growth of the House Sparrow and modelled this growth with a stage-structured matrix of two age classes (Figure 2). This model is equivalent to the model applied by Saether *et al.*, (1999). In the model only female birds are considered and the survival of females is assumed to be equal to that of males. We also assumed that breeding takes place in a pulse (cf. Caswell, 2001) in July and we censused the population in the model just after the young fledged (postbreeding  $p \downarrow 0$  in the notation of Caswell, 2001). The general formulation of the matrix model is given in Equation (1) and

$$\begin{pmatrix} J_n \\ A_n \end{pmatrix} = B(a, q, m) \begin{pmatrix} J_{n-1} \\ A_{n-1} \end{pmatrix} = \begin{pmatrix} b_{11} & b_{12} \\ b_{21} & b_{22} \end{pmatrix} \begin{pmatrix} J_{n-1} \\ A_{n-1} \end{pmatrix} = \begin{pmatrix} qm/2 & am/2 \\ q & a \end{pmatrix} \begin{pmatrix} J_{n-1} \\ A_{n-1} \end{pmatrix} \quad (1)$$



**Figure 2.** Schematic representation of the stage structured model. Class 1 represents the juveniles, the fledglings just after the breeding season and class 2 the adults from over one year of age. Last year's fledglings reproduce just before the census moment (postbreeding  $p \downarrow 0$ ). The transitions  $b_{11}$  and  $b_{12}$  comprise survival and reproduction,  $b_{21}$  and  $b_{22}$  only survival.

where  $m$  is the fertility value and equals the number of fledged juveniles per female per year,  $q$  the probability to survive the first year, and  $a$  the yearly survival from age one onwards. It should be noted that we assumed implicitly that the number of fledged juveniles per breeding female does not depend on the age of the breeding female. The entries on the first row of the projection matrix (1) describe the average number of fledglings that one female alive in the prior year produces in the next year. These are both non-zero matrix elements, because the juveniles that survive the first year reproduce before the next census. For both the juveniles and adults the number of female fledglings equals  $m/2$  and the probabilities to survive the year are  $q$  and  $a$  for juveniles and adults respectively. Matrix (1) models the post-breeding July population from year to year. Given an initial population in the different stage classes, the change over the years can be assessed by iterating projection matrix  $B$ . If the environment remains stable, the population size is determined by the absolute largest (= dominant) eigenvalue  $\lambda$  of the projection matrix (Caswell, 2001). This largest eigenvalue is the finite rate of population change:  $\lambda = e^r$ , where  $r$  is the instantaneous or intrinsic rate of population change. Here, the eigenvalue equals  $a + mq/2$ .

## 2.5. Elasticity Analysis

Caswell (2001) gives formulae for defining the elasticity of matrix entries ( $b_{ij}$ ) of the matrix  $B$  with ( $n$  columns and  $n$  rows,  $i = 1, \dots, n$  and  $j = 1, \dots, n$ ) in terms of the size of the dominant eigenvalue ( $\lambda$ ) of the matrix and its corresponding left ( $v = (v_1, \dots, v_n)$ ) and right ( $w = (w_1, \dots, w_n)^T$ ) eigenvectors. The elasticities of the matrix elements sum to 1.

$$e_{ij} = \frac{b_{ij}}{\lambda} \frac{\partial \lambda}{\partial b_{ij}} = \frac{b_{ij}}{\lambda} \frac{v_i w_j}{(v, w)} \quad (2)$$

The matrix entries in the first row result from functions of more than one lower level parameter ( $m, q, a$ ). These parameters are used for different matrix entries and thus a change in such a parameter will influence more than one matrix entry simultaneously. The elasticity of a lower level parameter (say  $y$ ) can be assessed with Equation (3)

(Caswell, 2001). Unlike the elasticities of the matrix elements the elasticities of lower level parameters do not sum to 1.

$$e(y) = \frac{y}{\lambda} \frac{\partial \lambda}{\partial y} = \frac{y}{\lambda} \sum_{i,j} \frac{\partial \lambda}{\partial b_{ij}} \frac{\partial b_{ij}}{\partial y} \quad (3)$$

More specific, the lower-level elasticities for  $a$ ,  $q$  and  $m$  for the general projection matrix are

$$e(a) = \frac{a}{\lambda} \left( \frac{m}{2} v_1 w_2 + v_2 w_2 \right) \quad (4a)$$

$$e(q) = \frac{q}{\lambda} \left( \frac{m}{2} v_1 w_1 + v_2 w_1 \right) \quad (4b)$$

$$e(m) = \frac{m}{\lambda} \left( \frac{q v_1 w_1 + a v_1 w_2}{2} \right) \quad (4c)$$

After computation of the elasticities it is easily shown that  $e(m) = e(q)$  for all values of  $m$ .

## 2.6. Count Data

We estimated the yearly population growth of the Dutch House Sparrow population on the basis of the counts given by CBS (2005), under the assumption that the index numbers based on the common bird census methods (see Figure 1) are proportional to the actual population size. The decline in the Index data (CBS, 2005) is most pronounced from 1990 onwards. To calculate the yearly growth factor the index in a particular year ( $i + 1$ ) is divided by the index of the prior year ( $i$ ). The growth factor clearly varies over the years, and to calculate the overall growth factor over  $n$  years the  $n$ th root is taken over the product of growth factors as in the standard formula for the calculation of a geometric mean (see Equation (5))

$$\sqrt[12]{\prod_{i=1990}^{2001} \frac{\text{Index}_{i+1}}{\text{Index}_i}} \quad (5)$$

## 2.7. Model Parameter Values

As stated, we first parameterised our general model with a range of survival values which vary between zero and one with a step-size of 0.01, and species specific reproduction data to understand the relative importance of the life history parameters on the finite rate of population change for a large part of the state space. Although the House Sparrow is a common bird, data on its breeding success in The Netherlands are lacking. Therefore we used data reported from Oxford, England (Seel, 1968a, b, 1970), which has comparable climatic conditions as The Netherlands, as an indication of the breeding success realised in The Netherlands. In the stable House Sparrow population the estimated number of fledglings per breeding pair per year equals 2.93 (see Table 2 for details according to Seel, 1968a, b, 1970). This estimate was computed as the product of clutch size, number of attempts per pair, egg survival, hatching success, and nestling survival (until fledging). For the declining period, no data on reproduction are available and

**Table 2.** Number of fledglings of the House Sparrow per pair per year.

Parameter	Value parameter (standard deviation)	Sample size
# eggs/nest <sup>a</sup>	3.98 (0.83)	831
# attempts/pair <sup>b</sup>	1.88	399
egg survival <sup>a</sup>	0.985	2963
hatching success <sup>a</sup>	0.877	2568
nestling survival <sup>a</sup>	0.454	2466
#fledglings/pair/year <sup>c</sup>	2.93	

<sup>a</sup>Seel (1968b).<sup>b</sup>Seel (1968a).<sup>c</sup>Seel (1970).

therefore we try a few different values in our analysis. Modelling only females implies that the output per breeding pair should be adjusted with the sex ratio. Literature data do not indicate that the sex-ratio of nestlings is biased. Therefore we assume a sex ratio of 1:1 (see  $m/2$  in the formulas for  $b_{11}$  and  $b_{12}$  in Equation 1). We supposed that the estimate based on the data of Seel (1968a, 1970) is a realistic mean estimate for the fertility of the Dutch House Sparrow and assumed that fertility varies from one to five realised fledglings per pair per year ( $m \in [1, 5]$ ). We evaluated the results of the general model using the survival estimates computed with MARK for the periods before and during the decline. In this way, we could diagnose the cause of the decline in The Netherlands.

### 3. RESULTS

#### 3.1. Statistical Analysis with MARK

The bootstrap goodness-of-fit test ( $P < 0.01$ ) of the general model ( $S_{(p,c)}$ ,  $F_{(p,c)}$ ,  $P_{(p,c)}$ ,  $r_{(p,c)}$ ) indicated relatively small overdispersion ( $\hat{c} = 1.16$ ). Therefore, we used the standard value of  $\hat{c} = 1$  and the  $AIC_c$  for further model selection and estimates of variance. Table 3 shows the nine candidate models of the 256 possible models that have an  $AIC_c$  weight  $> 0.01$ . As shown in the table the best performing models all have (sampling region) fidelity (F), recapture probability (p), and probability of being found dead and reported (r) as a functions of period. The model supported best discriminates the parameter survival for age-class irrespective of period. The quality of this model however, is not (very) different from the models that take survival as a constant, as a function of period, or as a function of both period and age-class ( $\Delta AIC_c < 2$ ). We used model averaging (Cooch and White, 2005) over the four best models (Table 3) to estimate adult and juvenile survival values. The results show juvenile and adult survival in the period of decline compared to the stable period (see Table 4).

#### 3.2. Finite Rate of Population Change ( $\lambda$ ) and Elasticity Analysis of the General Model

The model results on the finite rate of population change are given in the left panels of Figure 3. These graphs show contour plots of the dominant eigenvalue ( $\lambda$ ) of matrix (1) as a function of adult survival and juvenile survival for fertility values ( $m$ ) of one,

**Table 3.** Selected models for survival (S), site (sampling region) fidelity (F), recapture probability (p), and probability of being found dead and reported (r), being constant (.), period (p), age-class (c), or period and age-class (p, c) dependent for the House Sparrow in The Netherlands (explanation see methods section). The models used to estimate survival data are given in bold.

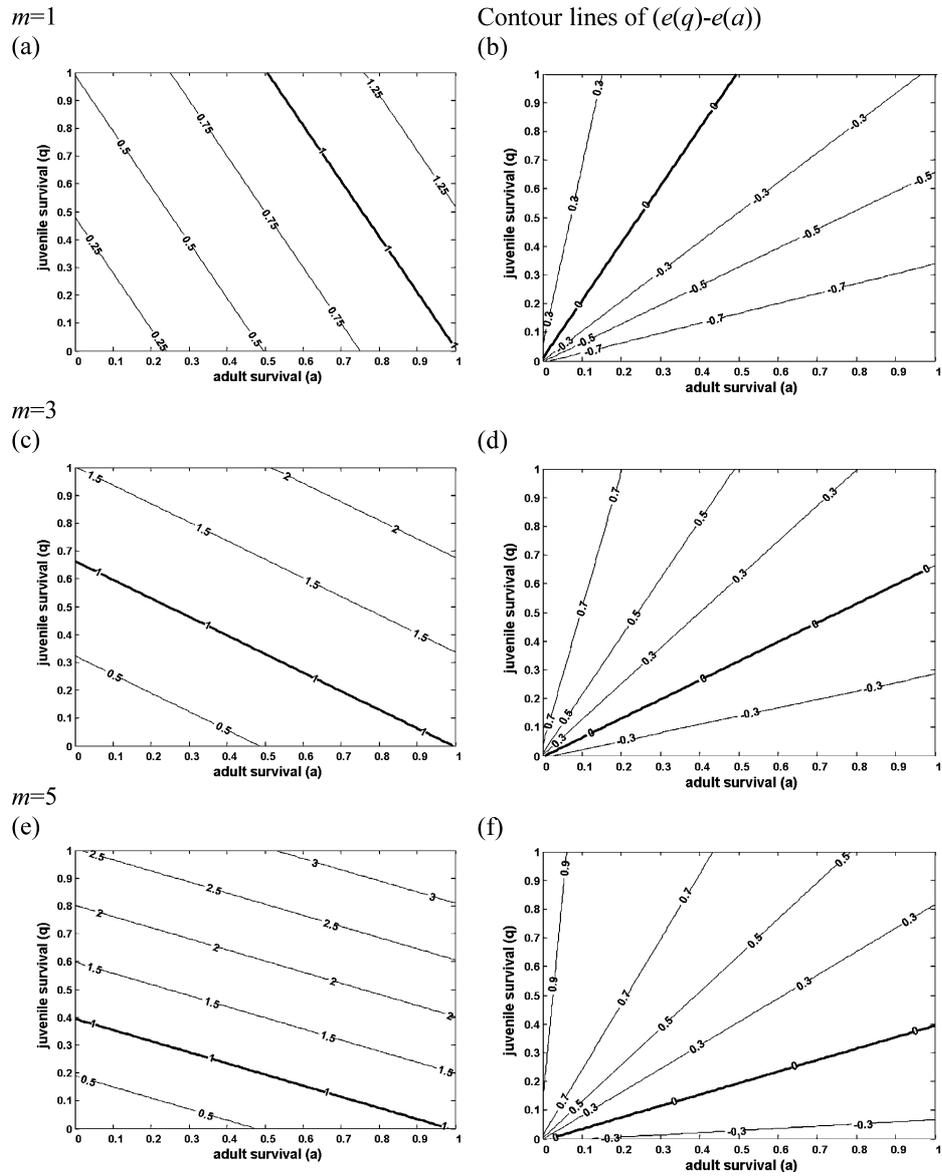
Model	$AIC_c$	$\Delta AIC_c$	$AIC_c$ weights	Model likelihood	No. of parameters	Deviance
<b>S<sub>(c)</sub>,F<sub>(p)</sub>,P<sub>(p)</sub>,r<sub>(p)</sub></b>	<b>2360.25</b>	<b>0.00</b>	<b>0.32</b>	<b>1.00</b>	<b>8</b>	<b>563.02</b>
<b>S<sub>(.)</sub>,F<sub>(p)</sub>,P<sub>(p)</sub>,r<sub>(p)</sub></b>	<b>2360.92</b>	<b>0.67</b>	<b>0.23</b>	<b>0.71</b>	<b>7</b>	<b>565.72</b>
<b>S<sub>(p)</sub>,F<sub>(p)</sub>,P<sub>(p)</sub>,r<sub>(p)</sub></b>	<b>2361.13</b>	<b>0.88</b>	<b>0.21</b>	<b>0.65</b>	<b>8</b>	<b>563.90</b>
<b>S<sub>(p,c)</sub>,F<sub>(p)</sub>,P<sub>(p)</sub>,r<sub>(p)</sub></b>	<b>2361.96</b>	<b>1.71</b>	<b>0.14</b>	<b>0.42</b>	<b>10</b>	<b>560.66</b>
S <sub>(c)</sub> ,F <sub>(p)</sub> ,P <sub>(.)</sub> ,r <sub>(p)</sub>	2363.42	3.17	0.07	0.21	7	568.22
S <sub>(.)</sub> ,F <sub>(p,c)</sub> ,P <sub>(p,c)</sub> ,r <sub>(p,c)</sub>	2366.31	6.06	0.02	0.05	13	558.87
S <sub>(p)</sub> ,F <sub>(p,c)</sub> ,P <sub>(p,c)</sub> ,r <sub>(p,c)</sub>	2367.80	6.55	0.01	0.04	14	557.30
S <sub>(c)</sub> ,F <sub>(p,c)</sub> ,P <sub>(p,c)</sub> ,r <sub>(p,c)</sub>	2368.09	7.84	0.01	0.02	14	558.59
S <sub>(p,c)</sub> ,F <sub>(p,c)</sub> ,P <sub>(p,c)</sub> ,r <sub>(p,c)</sub>	2369.59	9.34	0.01	0.01	16	555.97

**Table 4.** Survival estimates of the House Sparrow in The Netherlands based on averaging of all models with delta-AICc < 2 (see Table 3).

Period	Estimated parameter	95% CI		
		Mean	Lower	Upper
Stable 1976–1989	Sad	0.70	0.57	0.81
	Sjuv	0.66	0.51	0.78
Decline 1990–2003	Sad	0.66	0.56	0.75
	Sjuv	0.62	0.50	0.72

three and five fledglings per pair in 3a, 3c and 3e respectively. The interesting area in these graphs lies around the line where the dominant eigenvalue equals one. We give contour curves for more values to show that this dominant eigenvalue changes fast (slow) when the reproduction is high (low). For survival parameter combinations below the line  $\lambda = 1$  the population goes extinct, above this line the population is viable and will grow to infinity in the absence of limiting factors. The plots in the left panel indicate that with an increase in fertility the area below the curve  $\lambda = 1$  shrinks, as expected.

The right panels of Figure 3 show the elasticity results. These figures show contour plots of the difference between the elasticities of the juvenile and adult survival ( $e(q) - e(a)$ ), for fertility values of one, three and five fledglings per pair in Figures 3b, d and f, respectively. Actually since the elasticity of fertility is equal to that of juvenile survival the graph also shows the difference between fertility and adult survival. The area above the zero-contour indicates combinations of adult and juvenile survival where juvenile survival has a larger elasticity than adult survival ( $e(q) > e(a)$ ), whereas below the zero-contour this is reversed ( $e(q) < e(a)$ ). The contour plots show that with an increase in fertility the area below the zero-contour shrinks. The combination of the left



**Figure 3.** (a, c, e) Finite rate of population change (b, d, f) difference in elasticity of juvenile and adult survival for values of juvenile and adult survival ranging from zero to one and fertility ( $m$ ) equal to one, three and five, respectively.

and right panels indicate that for low values of fertility ( $m = 1$ , Figure 3a and b) in the area near  $\lambda = 1$  adult survival has a larger elasticity than juvenile survival. This is not the case for higher values of fertility. Here (Figure 3d and f) adult survival has a larger elasticity than juvenile survival only for parameter combinations of high adult survival and low juvenile survival.

### 3.3. Count Data

The growth rate of the House Sparrow population in The Netherlands as derived from the data from 1990 onwards as presented in Figure 1 and formula (5) equals 0.953, implying a decreasing population as is shown in the figure.

### 3.4. Diagnosis

Figure 4a summarises the results of the general model for  $m = 1, 3$  or  $5$  (drawn, dashed and dotted lines, respectively) representing parameter combinations for which the population growth factor equals one (4a) and lines representing parameter combinations for which the difference in elasticities between adult and juvenile survival is zero (4b). In these graphs our survival estimates from the Dutch House Sparrow before and during the decline are plotted. Like in Figure 3 a, c, e the area under the lines ( $\lambda = 1$ ) in Figure 4a represent parameter combinations where populations decline. The figure shows that only with a relatively low fertility value ( $m = 1$ ) the finite rate of population change is less than one ( $\lambda < 1$ ) in the period of population decline. With higher values of the fertility ( $m = 3$  and  $5$ ) the survival estimates both before and during the decline result in yearly population growth. Figure 4b indicates that with a low fertility value the estimated survival data fall within the region where adult survival has a larger elasticity than juvenile survival (i.e. below the drawn line), whereas for higher fertility values juvenile survival has the largest elasticity (above dashed and dotted line).

## 4. DISCUSSION

### 4.1. Statistical Analysis with MARK

Given the relatively small data set in the stable period (see Table 1) it is plausible that a model estimating separate survival estimates for the two periods does not perform better than one where the full period is treated as one. Also the confidence intervals of the survival estimates (Table 4) show considerable overlap. Therefore these survival estimates should be treated with caution. However, because the data on marked house sparrows from the Dutch Ringing Centre used in this study are the only available survival data, we have tentatively used the estimated survival values in our population study.

The estimates for House Sparrow survival from the analysis with MARK are relatively high compared to data from other sources (Table 5). However, these estimates are based on individuals marked and recovered or re-sighted in local populations. In local studies dispersal from the study site cannot be separated from mortality, and therefore survival estimates tend to be underestimated (Lebreton *et al.*, 1992). The studies of Siriwardena *et al.* (1999) and Freeman and Crick (2002) are based on ring-recovery data of marked individuals in Britain over the period 1962–1993 and 1965–2001 respectively, analysed with dead recovery models (Brownie *et al.*, 1985) in MARK (White and Burnham, 1999).

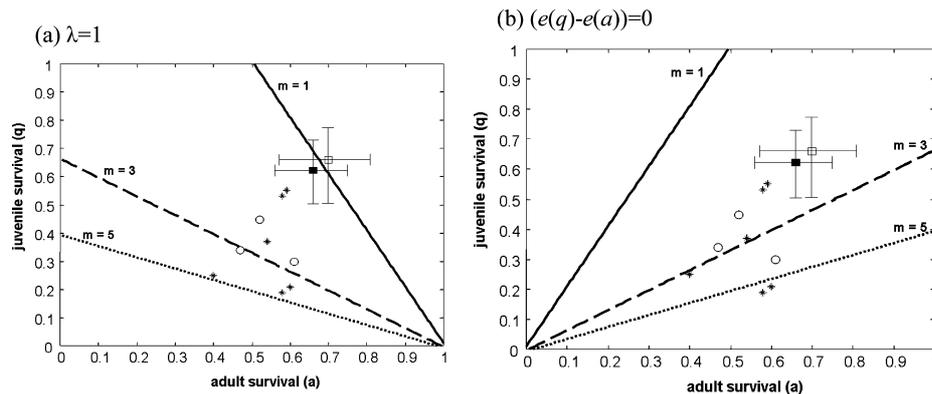
**Table 5.** Survival data of the House Sparrow from populations in Western Europe.

Juvenile survival mean (se)	Adult survival mean (se)	Country	Population	Source
–	0.58	Great-Britain <sup>a</sup>	Local	Summers-Smith (1956)
0.19	–	Great-Britain <sup>a</sup>	Local	Summers-Smith (1963)
0.25	0.40	Western Germany <sup>a</sup>	Local	Deckert (1969)
0.34–0.41	0.43–0.65	The Netherlands <sup>a</sup>	Local	Heij (1985)
0.53	0.58	Great-Britain <sup>a</sup>	Country	Freeman and Crick (2002)
0.55	0.59	Great-Britain <sup>a</sup>	Country	Siriwardena <i>et al.</i> (1999)
0.21 <sup>c</sup>	0.6 <sup>c</sup>	Norway <sup>a</sup>	Local	Saether <i>et al.</i> (1999)
0.66 (0.06)	0.70 (0.05)	The Netherlands <sup>a</sup>	Country	This study
0.45	0.52	Great-Britain <sup>b</sup>	Country	Siriwardena <i>et al.</i> (1999)
0.30	0.61	Great-Britain <sup>b</sup>	Country	Freeman and Crick (2002)
0.34	0.47	Great-Britain <sup>b</sup>	Local	Hole (2002)
0.62 (0.05)	0.66 (0.04)	The Netherlands <sup>b</sup>	Country	This study

<sup>a</sup>Non-declining population.

<sup>b</sup>Declining population.

<sup>c</sup>Arithmetic mean of data given in Saether *et al.* (1999).



**Figure 4.** (a) Parameter combinations for which the finite rate of population change equals one and (b) parameter combinations for which the difference in elasticities between adult and juvenile survival is zero of the general model for  $m = 1, 3$  or  $5$  (drawn, dashed and dotted lines respectively). Filled square the survival values from The Netherlands (declining period), open square (stable period) crosses 95% CI. Literature data on survival (see Table 5) open circles declining populations, and asterisks stable populations.

We report the results from the combined re-sighting and dead recovery data, because the fact that birds are seen alive contains the information that they had not died up to that age. Ignoring such (censored) data points would lead to an underestimation of survival (Bressers *et al.*, 1991). We also analysed the ring-recovery data of the Dutch House Sparrow in MARK with the data type “recoveries only”, and assessed lower estimates

for survival. Adult survival was underestimated by five percent, whereas juvenile survival estimates were one percent lower compared to the estimates based on the joint analysis.

Survival seems to be the demographic factor having caused the population decline of the British House Sparrow (Siriwardena *et al.*, 1999; Freeman and Crick, 2002; Newton, 2004). Freeman and Crick (2002) concluded from their analysis that first-year juvenile survival was lower in the period of decline whereas Siriwardena *et al.* (1999) suggested decline in both juvenile and adult survival as the most probable cause (see Table 5).

Our analysis with MARK suggests that the decline of the House Sparrow in The Netherlands may be qualitatively explained by lower survival values. Whether these lower values for survival can on their own account for the observed population decline has subsequently been investigated with a matrix population model.

## 4.2. Population Model Results

The general model results (Figure 3) show that for low fertility values ( $m = 1$ ) adult survival has the largest elasticity for most parameter combinations. For intermediate and high fertility values ( $m \geq 3$ ) the elasticity of  $\lambda$  for changes in juvenile survival is higher than that for adult survival in more than half of the parameter space. This implies that when fertility is low, adult survival in general has a higher impact on lifetime reproductive success and therefore on the finite rate of population change than juvenile survival. This pattern has been well established for other species (e.g. Charlesworth, 1980; Lebreton and Clobert, 1991; Heppel *et al.*, 2000; Saether and Bakke, 2000). Saether *et al.* (1999) studied a House Sparrow metapopulation on four islands in Norway over a period of three years. The growth rate ( $\lambda$ ) varied considerably over both years and islands, resulting from variation in reproduction and survival; however, the overall growth rate of this metapopulation was positive ( $\lambda = 1.05$ ). The elasticities of  $\lambda$  to variation in the different elements of the projection matrix differed strongly over both years and islands. Furthermore, the authors found that the elasticity of  $\lambda$  to changes in adult survival increased with decreasing  $\lambda$ , whereas its elasticity towards juvenile survival increased with increasing  $\lambda$ . These findings are in line with our result.

Presentation of the survival estimates resulting from MARK in the parameter space of juvenile and adult survival ranging from zero to one for three possible fertility values (Figure 4) makes clear that it seems unlikely that the reported lower survival can on its own account for the population decline. In addition, it seems reasonable to assume that also breeding success has decreased from the stable period to the period of population decline. In the absence of data on reproduction before and during the decline we deduce from the general model that decreased reproductive output in combination with decreased survival seems the most probable cause for the population decline.

For comparison, the survival estimates of stable and declining House Sparrow populations in Europe (see Table 5) are included in Figure 4. All these reported values are lower than our estimates from the data from the Dutch Ringing Center. Moreover, some stable populations (three lowest asterisks in Figure 4a) can according to our model only achieve growth rates above  $\lambda = 1$  for fertility values above  $m = 3$ . Some stable populations are even allowed to have a low reproduction of less than 3 fledglings per pair per year, whereas declining populations (open circles in Figure 4a) only decline if they have a low reproduction of less than 3 fledglings per pair per year.

For many threatened species conservation management plans cannot be based on insight derived from population models because detailed demographic information is unavailable. In these cases elasticity analysis can be a qualitative guide for research and management (Heppell *et al.*, 2000).

As shown in the example of population decline in the House Sparrow in The Netherlands, combining information on the general pattern of  $\lambda$  and elasticities with scarce information on changed vital rates can be helpful to identify whether or not the vital rate for which information is lacking should have changed.

For the House Sparrow in The Netherlands we strongly advocate the need for further research on reproduction, because information on this vital rate in combination with Figure 4 can indicate whether it is better to improve adult or juvenile survival.

In our analysis we assumed density independent population growth in the House Sparrow and modelled this with a deterministic matrix model parameterized with average vital rates. Obviously, life-history values may vary over time which would advocate the use of a stochastic model to assess growth rates and elasticities. In general, deterministic growth rates overestimate long-term stochastic growth rates, with the bias increasing with the variability in vital rates (Tuljapurkar, 1990; Caswell, 2001), elasticity patterns of stochastic matrix models, however, are usually very similar to the patterns of deterministic models (Benton and Grant, 1996; Caswell, 2001; Silvertown and Charlesworth, 2001). Although stochastic elasticities may be different from deterministic ones if variation results in large deviations of the stochastic matrices from the mean (deterministic) matrix (Morris and Doak, 2004) the ranking of stochastic elasticities deviate from deterministic ones only if the life-history graph contains alternative pathways (e.g. plants with a generative and a vegetative mode of reproduction) (Claessen, 2005). This implies that our results on elasticities are robust to assumptions on variation in life-history values, whereas the result on growth rates is overestimated. Including stochasticity however, can only be done if more detailed information is available on vital rates, especially on the variance of these over the years. House sparrows in The Netherlands seemingly have not been perceived as an interesting species by many birders given that even ringing data are scarce and reproduction data are absent with the exception of some local populations over a relatively short time span (Heij, 1985). Therefore, including stochasticity is as yet not feasible. To cite Doak *et al.* (2005) 'It can be much more useful to have a prediction of the most optimistic likely outcome than it is to have such an uncertain, but unbiased, prediction that it can support few or no conclusions at all.'

### 4.3. Conservation Measures

Which environmental factors should be improved and how can this be accomplished? This obviously depends on the actual reproductive rate for which data are lacking. On the basis of our model assessment and survival analysis, some factors, suggested to have caused the decline in urban areas can be discarded. Suggested causes in the literature indicate (1) low winter food levels, (2) low number of nesting places, (3) scarce nesting material, (4) scarce food for nesting birds and (5) high predation rate. Of these factors survival will be influenced by (1), and (5), whereas (2), (3), (4) and (5) can reduce reproduction.

Low winter food levels are claimed to have caused a decline in many farmland bird species (Peach *et al.*, 1999). Also in cities historic data indicate a strong correlation

between food abundance and population density. This is illustrated by Bergtold (1921) who claimed that at the start of the last century decrease in food abundance has resulted in a dramatic decline of House Sparrow populations following the displacement of horse drawn transport by motor vehicles. Little is known on the actual predation rate in the House Sparrow. Predation may have increased resulting from a general increase in birds of prey since their drastic decline over the period 1950–70 (Kjellen and Roos, 2000), and an increase in domestic cat ownership (Crick *et al.*, 2003). The role of the domestic cat as a predator may have been largely underestimated as shown by Churcher and Lawton (1987) who estimated that domestic cats cause 30% of the total mortality in house sparrows.

The frequency distribution of dead recoveries of adults shows no higher recovery rate in winter. On the contrary, the data seem clumped in the breeding season. Therefore, it seems unlikely that low food levels in winter caused the decrease in adult survival. Also high predation rate does not seem a very probable factor, since increased predation is expected to have a larger impact on juvenile than adult survival, whereas the relative decrease in adult survival was higher than in juvenile survival.

Reproduction can be improved by either increasing the participation of birds in reproduction or enhancing the performance per pair. The participation in breeding may be limited by the number of available nesting places if the number of nesting places is outnumbered by the number of potential breeders. In such cases increasing the number of nesting places by providing artificial nest sites can increase the reproductive output of the population. However, if fledgling production per pair is too low, such that a individual no longer replaces itself in its lifetime, increasing the number of nest sites has no beneficial effect on the finite rate of population change. Breeding performance per pair may be limited by shortage of insect food for the nestlings as suggested by Summers-Smith (1988, 1999). Improving food conditions may therefore enhance breeding performance.

Summarising, we advise to increase the number of nesting places and enhance breeding performance by improving the food availability for the nestlings of the House Sparrow.

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